SPECIATION BY ANEUPLOIDY AND POLYPLOIDY IN *MIMULUS* (SCROPHULARIACEAE)[1]

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Speciation by aneuploid and polyploid changes in chromosome numbers is so common in flowering plants as to be almost a characteristic of the angiosperms. Elegant examples of these patterns of evolution are exhibited by monkey flowers of the genus *Mimulus* (Scrophulariaceae).

The genus *Mimulus* contains some 150 species occurring in western North and South America with a few outlying species in eastern North America, Japan, Vietnam, the Himalayas, New Zealand, Australia, and South Africa. The center of diversity is California, with a secondary center in Chile. Some species are annuals of deserts, grasslands, or forests; some are biennials of marshy places; some are herbaceous perennials from springs, streamsides, or lake-shore habitats; and others are woody shrubs of the dry California chaparral. The species form clusters reflecting these various life forms. There are 8–10 such clusters commonly recognized as sections of the genus *Mimulus* (Grant 1924, Pennell 1951, Chuang and Heckard personal communication).

Chromosome numbers of over 50 species (Table 1), that is, approximately one-third of the *Mimulus* species, have been ascertained by Vickery and his co-workers (Vickery 1978, Vickery, Chu et al. 1981, Vickery, Simpson et al. 1981, Vickery et al. 1982, 1985, 1986, 1990, unpublished) and by Chuang and Heckard (personal communication). Chromosome numbers reveal intriguing patterns of evolution by aneuploidy and polyploidy.

First, let us consider the base chromosome numbers of the eight main sections of the genus. Section *Mimulastrum* has a base number of $x = 7$; *Eunanus* and *Erythranthe* have base numbers of $x = 8$; *Paradanthus* 8, 9, 10; *Eumimulus* 8, 11, 12; *Oenoe* 9; *Diplacus* 10; and *Simiolus* 14, 15, 16, 30. Base numbers of the sections suggest extensive evolution by both aneuploidy and polyploidy. For the genus as a whole, the base number appears to be $x = 8$, inasmuch as the other plausible base number, $x = 7$, is found only in one, apparently derived, desert species, *M. mohavensis* Lemmon (Table 1).

Next, let us consider the chromosome numbers by individual species. All species counted thus far are the same in each of several sections, specifically, in *Mimulastrum*, *Erythranthe*, *Oenoe*, and *Diplacus*. The other sections are polymorphic for their species' chromosome numbers and frequently exhibit speciation by aneuploidy and/or polyploidy, often in complex combinations. For example, the various species of section *Eumimulus* exhibit $n = 8$, 11, and 12; species of section *Eunanus* exhibit $n = 8$, 10, and 16; species of section *Paradanthus* exhibit $n = 8$, 9, 16, 17, 18, and 30; and species of section *Simiolus* exhibit $n = 13$, 14, 15, 16, 24, 28, 30, 31, 32, 46, and 48 (Table 1).

Section *Simiolus*, which shows by far the most speciation by aneuploidy and/or polyploidy of all sections of the genus, consists of six species groups, that is, complexes of related species and varieties. First is the *M. guttatus* complex, centered in California; it has as its base number $x = 14$, with aneuploid forms at $n = 13$ and $n = 15$ (Table 1), as well as tetraploid forms with $n = 28$. Second is the alpine (western United States) *M. tilingii* complex with its base number of $x = 14$ and aneuploid forms at $n = 15$, $n = 16$, and an unusual polyploid form at $n = 24$. The third species group is the *M. dentilobus* complex of southwestern United States and northwestern Mexico with its base number of $x = 16$ and an aneuploid form at $n = 15$. Fourth is the *M. luteus* complex

TABLE 1. Chromosome numbers in the genus *Mimulus* by sections (counts by Chuang and Heckard and by Vickery and co-workers; see text for references).

Taxon	$n =$
Mimulastrum Gray ($x = 7$)	
M. mohavensis Lemmon	7
Eumimulus Gray ($x = 8, 11, 12$)	
M. alatus Aiton	11
M. gracilis R. Br.	8
M. ringens L.	8, 12
Eunanus Gray ($x = 8$)	
M. bolanderi Gray	8
M. layneae (Greene) Jepson	8
M. brevipes Bentham	8
M. cusickii (Greene) Piper	8
M. nanus Hook. & Arn.	8
M. torreyi Gray	10
M. biglovii Gray	16
Paradanthus Grant ($x = 8, 9, 10$)	
M. bicolor Hartweg ex Bentham	8
M. filicaulis Watson	8
M. breweri (Greene) Coville	16
M. floribundus Douglas	16
M. moschatus Douglas	16
M. latidens (Gray) Greene	16
M. arenarius Grant	16
M. primuloides Rydb.	9, 17, 18
M. repens R. Br.	10
M. nepalensis Bentham	16, 30
Erythranthe Greene ($x = 8$)	
M. cardinalis Douglas	8
M. eastwoodiae Rydb.	8
M. lewisii Pursh	8
M. nelsonii Grant	8
M. rupestris Greene	8
M. verbenaceus Greene	8
Oenoe Gray ($x = 9$)	
M. pictus (Curran) Gray	9
M. tricolor Lindl.	9
M. pygmaeus Grant	9 (or 10?)
M. pilosellus Greene	9
Diplacus Gray ($x = 10$)	
M. aridus (Abrams) Grant	10
M. aurantiacus Curt.	10
M. calycinus Eastw.	10
M. clevelandii Brandg.	10
M. fasiculatus (Pennell) McMinn	10
M. longiflorus (Nutt.) Grant	10
M. puniceus (Nutt.) Steud.	10
Simiolus Greene ($x = 14, 15, 16$)	
M. gutatus Fischer ex DC.	14, 15, 28
M. laciniatus Gray	14
M. nasutus Greene	13, 14
M. glaucescens Greene	14
M. platycalyx Pennell	15
M. tilingii Regel	14, 15, 24, 28
M. genniparus Weber	16
M. dentilobus Rob. & Fern.	15, 16
M. wiensii Vickery	16
M. glabratus HBK	15, 30, 31
M. andicolus HBK	46
M. pilosiusculus HBK	46
M. externus (Skotts.) Skotts	46
M. luteus L.	30, 31, 32
M. cupreus Dombrain	31
Undescribed	
n. sp #A	16
n. sp #B	32
n. sp #C	32, 48 ± 1–4

from the central and southern Andes of South America. Its base number is $x = 30$, but there are $n = 31$ and $n = 32$ forms as well. Fifth, there is the *M. glabratus* complex that ranges from Canada to Patagonia. Its varieties in central North America exhibit the base number of the complex, $x = 15$. In the Rio Grande drainage we find tetraploids with $n = 30$. From northern Mexico to southern Colombia we find the aneuploid tetraploid $n = 31$ varieties of the complex. From Ecuador south to southern Argentina and including the Juan Fernandez Islands off the coast of Chile, we find the aneuploid hexaploid species and varieties with $n = 46$ chromosomes. Apparently, each change in chromosome number facilitated an adaptive radiation further south. Last is the *M. wiensii* complex of the mountains of western Mexico with its base number of $x = 16$ and three apparent new species that are morphologically distinct and reproductively isolated (Vickery et al. unpublished). One has $n = 16$ chromosomes, one has $n = 32$ chromosomes, and the third has two forms—one with $n = 32$ chromosomes and the other with $n = 48 \pm 1$–4 chromosomes (incipient aneuploidy?).

How does speciation by aneuploidy and polyploidy occur? We carefully examined meiosis in *M. glabratus* var. *utahensis* and *M. glabratus* var. *fremontii*, two of the widespread diploid varieties of the *M. glabratus* complex, and their intervarietal F_1 hybrids. First, of 1317 cells examined in diakinesis or metaphase of first meiosis (Tai and Vickery 1970, 1972), 1090 exhibited regular 15 bivalent chromosomes. Another 23 cells, or 1.7%, had aneuploid numbers of chromosome pairs ranging from only 6 to as many as 13, plus 4–18 univalents. These cells presumably could produce aneuploid gametes, at least in some cases. A sizeable minority, 204 cells, exhibited 14 II and 2 I, or 13 II and 1 IV, or complement fractionation with its uneven groupings of chromosomes. These cells might produce aneuploid gametes also. Second, of 782 additional cells observed in Anaphase I, 294 (37.5%) exhibited unequal disjunction, laggard chromosomes, or chromatin bridges. These cells also could result in aneuploid gametes. Some 47 of these abnormalities occurred in *M. glabratus* var. *fremontii*, only 18 occurred in *M. glabratus* var. *utahensis*, but most, 229, occurred in the intervarietal hybrids. Thus, varieties differ in their potential for producing aneuploid gametes,

and intervarietal hybrids are particularly prone to do so. This suggests to me that natural hybridization probably plays a significant role in evolution in monkey flowers. Finding occasional plants in various populations with aneuploid chromosome numbers indicates that aneuploid gametes not only are produced, but actually function. Third, of 95 cells examined in Anaphase II, 22 were polyploid and could presumably lead to polyploid gametes. Thus, we see significant numbers of the very cytological abnormalities in the basic diploid varieties that could lead to evolution by aneuploidy and polyploidy, that is, to the very patterns of evolution that we actually see in the *M. glabratus* complex.

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